CHIASMA STUDIES IN PLANTS, I. CHROMOSOME PAIRING AND CHIASMA BEHAVIOUR IN *ALLIUM MOLY**

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With 14 Text-figures

To explain chiasmata, there have been two hypotheses advanced, namely the alternate opening out hypothesis ('classical theory', 'McClung's theory') and the (partial) chiasmatype hypothesis. Sax, K. (1930, 1932) advocated the former combined with the inclusive theory of subsequent breakage at the cross of the chiasma, while Belling (1931, 1933) and Darlington (1930, 1932) independently put forward the latter hypothesis. The present paper reports in part the results obtained from observations made during this series at chiasma studies in plants.

OBSERVATIONS

The root-tips were fixed in Karpechenko's solution and the pollen mother cells in Bouin's fluid after being treated in Carnoy's mixture for two or three minutes. The paraffin sections were cut from twelve to twenty micra in thickness. For the staining Newton's gentian violet method was employed in the case of both root-tips and pollen mother cells.

Fig. 1. Somatic mitosis in a root-tip cell of *Allium Moly* ($2n=14$) and a diagram to show relative lengths of mitotic chromosomes. $\times 1900$.

Mitosis. The somatic number of chromosomes is fourteen in this species. All chromosomes have conspicuous median or submedian constrictions. The length relation of the chromosomes is shown in Fig. 1.

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Meiosis. At the pachytene stage the chromosomes seem to be paired normally by every chromomere as pointed out by Belling (1928, 1931) (Fig. 2). In *Agapanthus* (Belling 1928 ; Darlington 1933), the chromosomes were

Fig. 2. A, B, Nuclear threads in the early pachytene stage in *Allium Moly*. C, D, Late pachytene. The total number of chiasmata is given under each figure. $\times 1900$.

condensed in the neighbourhood of the spindle fiber attachment, but in *Allium* this localized condensation is not observed. The condensation of the chromosomes seems to be spiralisation (cf. Darlington 1933), and Fig. 2. A is suggestive of this. In the late pachytene and the early diplotene stages, the nodes or chiasmata are distributed evenly among the pairs of chromosomes (cf. Levan 1933 ; Moffett 1932). At the diplotene stage, the quadruple nature of the bivalents is not clearly seen as Levan observed in *Allium fistulosum*, but it can be observed at points of subterminal chiasmata and opening loops. The terminal chiasmata were rare at this stage and the sparseness of chiasmata (Figs. 4, 5, 6) conveyed an impression of the sliding of the cross of a chiasma toward the ends of the chromosomes or the slipping off of the terminal chiasma at the end, sometimes indicating the long distal arms. I use the expression 'terminalisation' in the above sense (cf. Satô, D. 1934). In the early diaphase, which is termed late diplotene by Darlington and his collaborators, the secondary split of a bivalent can be clearly ascertained (Figs. 7-9). The reduction of chiasmata seems to depend upon the opening out or slipping off of terminal chiasmata (Moffett 1932). In the late diaphase, the neighbouring internodes tend to become perpendicular to each other on account of conspicuous contraction of the chromosomes (Figs. 10, 11). Many chiasmata were lost between the diplotene stage and the late diaphase and the terminalisation was incomplete (cf. *Fritillaria*, Darlington 1930 ; *Tulipa*, Darlington and Janaki-Amnal 1932 ; *Stenobothrus*, Darlington and Dark 1932) (Tables 1, 2). (For the definition of the terms used in this paper, cf. Satô 1934). At the metaphase and in the early anaphase the configurations have commonly two compensating (symmetrical) chiasmata perhaps due to their having median and submedian spindle fiber attachments.

Figs. 3-14. Bivalents from nuclei at the first meiotic division in the pollen mother-cells of *Allium Moly*. $\times 1900$. 3, Early diplotene. 4, Mid-diplotene. 5, Late diplotene. 6, Diplotene. The configurations have only small loops in A-C, both small loops and large median loops in D-I, all large loops or large subterminal loops in J-N, a large terminal loop in O, and long distal arms in P-S. 7, 8, Early diaphases. 9, Early diaphase, indicating the process of slipping off of chiasmata. 10, Late diaphase. 11, Early metaphase. 12, Metaphase. 13, Anaphase. 14, Separation process of chromosomes with subterminal spindle fiber attachment.

Table 1 Distribution of chiasmata in *Allium Moly*

Stage \ Xta	1	2	3	4	5	6	7	8	9	10	11	12	Total bivalents
Diplotene	—	1	5	11	23	29	24	15	9	5	2	2	126
Early diaphase	3	23	38	39	18	5	—	—	—	—	—	—	126
Late diaphase	3	30	22	8	—	—	—	—	—	—	—	—	63
Metaphase	11	90	22	3	—	—	—	—	—	—	—	—	126
Early anaphase	23	39	1	—	—	—	—	—	—	—	—	—	63

Table 2

Stage	No. of Cell	No. of Biv.	No. of Xta.	Xta Cell	Xta Biv. (M)	Variance (σ)	$\frac{\sigma}{M}$	No. of Term. Xta	Term. Xta Biv.	Term. Coeff.
Diplotene	18	126	815	45.28	6.469	1.926	0.297	19	0.158	0.023
Early diaphase	18	126	439	24.39	3.484	1.132	0.324	41	0.325	0.093
Late diaphase	9	63	161	17.88	2.555	0.708	0.277	23	0.365	0.143
Metaphase	18	126	269	14.94	2.135	0.582	0.272	71	0.564	0.264
Early anaphase	9	63	104	11.55	1.651	0.509	0.308	56	0.888	0.538

The fusion of chiasmata occurs very rarely, actually only when more than two chiasmata exist in one arm of the bivalent (as in *Zea mays*, Darlington 1934). This fusion of chiasmata is different from the "break-and-join" of the crossed chromatids at the chiasma which results in the genetical crossing-over. Such break-and-join does not seem to occur in this case of *Allium* which therefore conflicts with Sax's opinion.

The present observation in *Allium* suggests that crossed chromatids were lengthened and that the double spiral of chromonemata would not disturb the terminalisation (cf. Levan, 1933; Figs. 8, 9). Accordingly, the reduction in number of chiasmata may be chiefly due to the slipping off of chiasmata or terminalisation. The results obtained in the present work together with those obtained with other plants will be discussed in detail in the second report of this series (D. Satô, 1934).

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